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ORIGINAL PAPER

Communication in troubled waters: responses of fish communication systems to changing environments

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Abstract Fish populations are increasingly being subjected to anthropogenic changes to their sensory environments. The impact of these changes on inter- and intra-specific communication, and its evolutionary consequences, has only recently started to receive research attention. A disruption of the sensory environment is likely to impact communication, especially with respect to reproductive interactions that help to maintain species boundaries. Aquatic ecosystems around the world are being threatened by a variety of

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environmental stressors, causing dramatic losses of biodiversity and bringing urgency to the need to understand how fish respond to rapid environmental changes. Here, we discuss current research on different communication systems (visual, chemical, acoustic, electric) and explore the state of our knowledge of how complex systems respond to environmental stressors using fish as a model. By far the bulk of our understanding comes from research on visual communication in the context of mate selection and competition for mates, while work on other communication systems is accumulating. In particular, it is increasingly acknowledged that environmental effects on one mode of communication may trigger compensation through other modalities. The strength and direction of selection on communication traits may vary if such compensation occurs. However, we find a dearth of studies that have taken a multimodal approach to investigating the evolutionary impact of environmental change on communication in fish. Future research should focus on the interaction between different modes of communication, especially under changing environmental conditions. Further, we see an urgent need for a better understanding of the evolutionary consequences of changes in communication systems on fish diversity.

Keywords Evolution · Environmental change · Sensory systems · Sexual selection · Phenotypic plasticity · Adaptation

Introduction

Most fishes experience natural variation in environmental conditions across spatial and temporal scales, but the speed and severity of these changes has recently increased. Aquatic biodiversity is globally threatened by anthropogenic disturbance of the environment (Ricciardi and Rasmussen 1999; Malmqvist and Rundle 2002; Donohue and Molinos 2009). The fate of all organisms under these new conditions will depend largely on their ability to respond to environmental changes through adaptive dispersal, plasticity, or evolution (Stockwell et al. 2003). Thus far, research has found that animals facing human-induced environmental change show greater phenotypic (and often genetic) changes than do those experiencing more natural environmental variability (Hendry et al. 2008; Darimont et al. 2009). While most recent work has focused on the evolutionary effects of fisheries (e.g. Law 2007; Sharpe and Hendry 2009), another major effect is alteration of the sensory environment. In this case, we might expect impacts on a multitude of inter- and intra-specific interactions such as predator–prey relationships, species recognition, and reproductive activities. Here, we explore current understanding of how changing environmental conditions will influence future fish biodiversity by considering the impact of altered environments on the communication systems of fishes.

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Since communication between individuals is one of the key pre-mating reproductive barriers between species, changes to the sensory environment should strongly influence the origins and maintenance of species diversity. We therefore focus on studies of reproductive interactions: e.g., inter- and intra-specific mate selection or male-male competition. The effects of environmental change on other forms of inter-specific interactions, for example the influence of turbidity (light-scattering and -absorbing suspended particles) on visual interactions between predators and prey, have been discussed elsewhere (e.g., Utne-Palm 2002; Domenici et al. 2007).

The sensory environment is the interface between sending and receiving signals; animal communication systems thus evolve under a specific environmental regime (Endler 1992). By communication "systems", we mean the combined expression, transmission, and reception of signals in the visual, chemical, acoustic, or electric modalities. Changes to the sensory environment can influence animal communication by altering the *expression* of the signal at the sender level (e.g., endocrine disrupting chemicals altering the expression of sexually selected ornamentation; Baatrup and Junge 2001), by altering the *transmission* of the signal (e.g., noise pollution masking acoustic signals; Slabbekoorn and Peet 2003), or by altering the ability of an animal to *receive* the signal due to shifts in receptor sensitivity (e.g. increased turbidity and changes to wavelength composition driving shifts in visual sensitivity; Hofmann et al. 2009). In many cases, we expect human-induced environmental change to degrade the sensory environment by masking signals and their reception. This altered sensory "scene" can inhibit an animal's ability to sense and learn from its environment and thus affect communication specifically, and survival in general (Fay and Popper 2000). However, environmental change can also enhance communication, and possibly lead to novel communication traits or change the traits that are under selection. We tend to focus here on the potential degrading effects of environmental change as this has led to the loss of fish biodiversity (e.g., Seehausen et al. 1997) and is the cause of conservation concern.

The evolution of communication systems used in fish reproduction is complex: signals and sensory systems can be acted upon independently by processes of natural and sexual selection (Andersson 1994), as well as being under correlational selection (Brooks and Couldridge 1999). Furthermore, the expression and reception of signals can be genetically based or plastic through (for example) condition dependence (i.e., higher condition leads to greater trait elaboration; Price 2006). Changes in the sensory environment can also affect the strength and direction of natural and sexual selection, disrupting the balance between them and leading to a change in evolutionary trajectories. We might also expect plasticity of communication traits to be under strong selection itself, since plasticity may promote rapid evolution in severely altered environments (Lande 2009). In addition, spatial and temporal variation in natural and sexual selection is expected to be strong (Siepeilski et al. 2009; Svanback et al. 2009) and can thus have strong influences on the evolution of genetic and plastic variation. Because of these complexities, predicting the responses of fish to environmental change is a challenge, but one worth undertaking given the pace and severity of environmental changes associated with human activities.

Here, we outline our current understanding of how fish communication is influenced by changing environments by summarizing key informative examples (Fig. 1; Table 1) and giving a conceptual overview of the relationships between human-induced environmental change and communication systems (Fig. 2). We discuss the possible evolutionary implications of environmental changes for communication systems and for fish diversity, highlight directions for future research, and briefly discuss the extent to which such research could inform conservation.

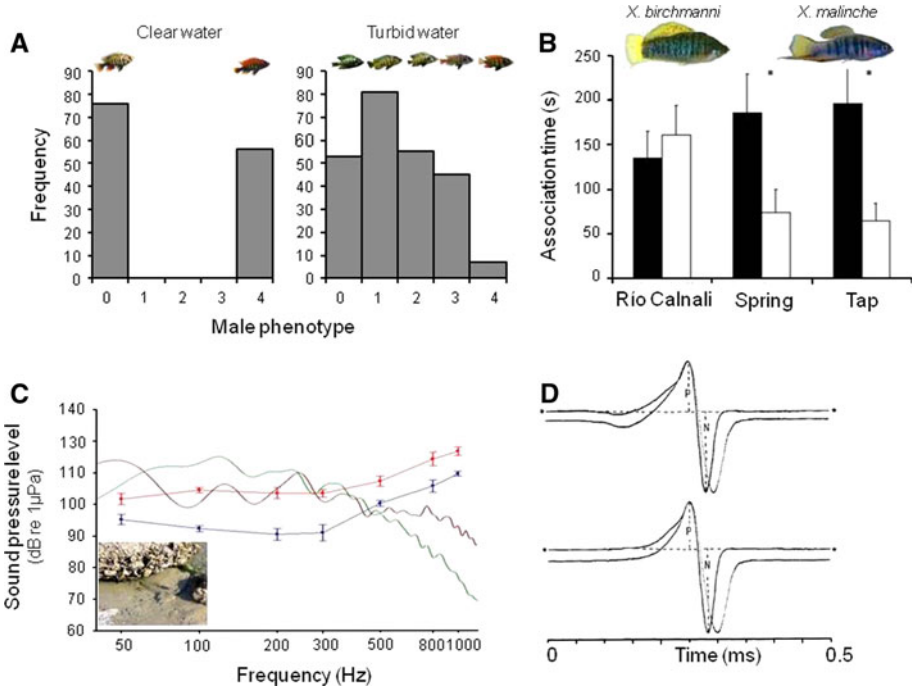

Fig. 1 Examples of studies showing responses to environmental variation in the sensory environment. **a** *Left panel*: male phenotype distribution of a species pair of Lake Victoria cichlids, *Pundamilia pundamilia* (left photo) and *P. nyererei* (right photo), in clear water. *Right panel*: male phenotype distribution in turbid water, showing the collapse of the species pair (modified from Seehausen et al. 2008) (With permission from MacMillan Publishers Ltd.: Nature). **b** Female swordtail fishes, *Xiphophorus birchmanni* (left photo) and *X. malinche* (right photo) prefer chemical cues of conspecific males (*black bars*) over heterospecific males (*white bars*) in clean water (spring, tap water) but failed to show preference in stream water polluted with sewage and agricultural runoff (see Fisher et al. 2006) (With permission from the RoyalSociety). **c** Mean (±SE) hearing thresholds of the Lusitanian toadfish, *Halobatrachus didactylus* (photo), in the presence of ambient (*blue line*) and ship (*red line*) noises. The power spectra (frequency vs. amplitude) of the mate attraction call (boat whistles, *green line*) and the agonistic grunt train (*brown line*) are also depicted. Sound detectability decreased dramatically in the presence of ship noise (for details see Vasconcelos et al. 2007) (With permission from the authors). **d** Electric organ discharge of two related weakly electric fish *Campylomorrnyrus tamandua* (top) and *C. rhynchophorus* (bottom): the same individuals measured at high conductivity (*solid line*, indicated with an *asterisk*) and after 70 h exposure to low conductivity (*dotted line*) (modified from Kramer and Kuhn 1993) (With permission from Springer Science + Business Media)

Modes of communication: evidence for change?

Visual

Studies of fish communication, focused on evolutionary diversification, tend to emphasize visual signals associated with choosing or competing for mates (e.g., cichlids, sticklebacks, guppies; Endler 1983; Seehausen et al. 1997; Boughman 2001; Albert et al. 2007; Kemp et al. 2008; Seehausen et al. 2008). The efficacy of visual signals depends on the amount (intensity) and spectral composition (colour) of light incident upon the signaller, reflection from the surface of the signaller, transmission through the medium, background light, and detection by the visual system of the receiver. If the intensity or colour of available light is

Table 1 Examples of how communication systems respond to disturbance of the aquatic environment

Sensory modality	Stressor	Response	Evolutionary change	System(s)	References
Visual	Turbidity	Change in male colouration	Yes	African cichlids, Sticklebacks	(Seehausen et al. 1997; Wong et al. 2007)
		Increased cost of mating and loss of conspecific mate preference	Yes	Sticklebacks	(Candolin et al. 2007)
	Chemical	Change in aggressive behaviour	?	Sticklebacks	(Bell 2001)
		Change in male colouration	?	Guppies	(Baatrup and Junge 2001)
	Flow regime	Change in nest shape	?	Sticklebacks	(Rushbrook et al. 2010)
Chemical	Chemical	Loss of conspecific mate preference	Yes	Swordtails	(Fisher et al. 2006)
		Loss of pheromone detection resulting in lowered fertilization success	?	Atlantic salmon	(Moore and Waring 2001)
		Reduction in reproductive behaviour	?	Brown trout	(Jaensson et al. 2007)
		Avoidance of conspecifics, loss of shoaling behaviour	?	Banded killifish	(Ward et al. 2008)
	Eutrophication	Increased pH enhances female preference for male odour cues	?	Sticklebacks	(Heuschele and Candolin 2007)
Acoustic	Noise	Temporary or permanent hearing loss	?	Atlantic cod, Goldfish, Oscar, Pink snapper	(Reviewed in Popper and Hastings 2009)
		Temporary shift in hearing thresholds	?	Northern pike, Lake chub, Rainbow trout, Goldfish, Fathead minnow, Lusitanian toadfish	(Reviewed in Vasconcelos et al. 2007; Popper and Hastings 2009)
Electric	Temperature	EOD rate increases with increasing temperature	?	*Brachyhypopomus pinnicaudatus*	(Silva et al. 2007)
		Change in EOD frequency, amplitude, and waveform	?	*Apteronotus leptorhynchus*	(Dunlap et al. 2000)

Table 1 continued

Sensory modality	Stressor	Response	Evolutionary change	System(s)	References
	Conductivity	Change in EOD parameters in sister species, species-specific differences remained	?	Dwarf stonebashers	(Baier 2008)
		Change in communication range	?	*Brienomyrus niger*	(Squire and Moller 1982)
Multimodal	Turbidity	Switch from vision to olfaction for mate choice	Yes	Sticklebacks	(Heuschele et al. 2009)

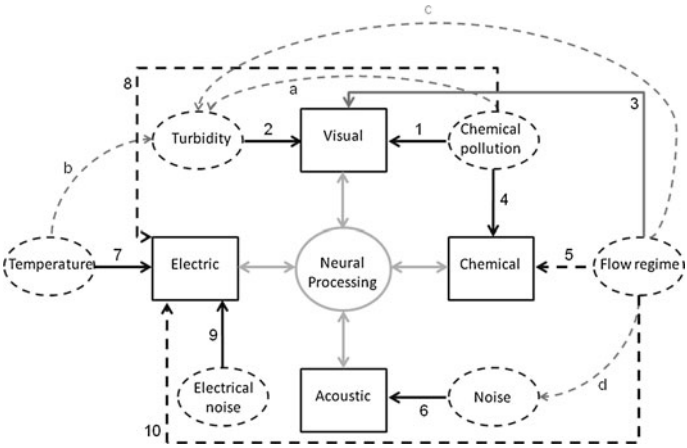

Fig. 2 Relationships between human-induced environmental changes and communication systems in fish. At least four modes of communication (vision, chemical, acoustic, electric) are important for fish; the signals and reception of those signals can be compromised by a number of environmental factors rapidly altering global aquatic systems. *Numbered arrows* show direct influences (*solid*) or possible influences (*dashed*) of factors on each sensory modality (see text). *Lettered arrows* show possible influences of one factor on another, i.e. indirect influence on a communication modality. Chemical pollutants (**a**), changes in water temperature due to climate change or point source industrial inputs (**b**), and altered flow regimes (**c**) can promote algae growth and sedimentation, increasing turbidity and thereby indirectly affect visual communication (2). Alteration of the flow regime can increase noise (**d**) and thereby affect acoustic communication (6). All communication modalities are linked through central neural processing and are not functioning independently

altered due to, for example, suspended particles that scatter the light, visual communication will be compromised. Thus, if we know the spectral content of a signal, properties of transmission through the water, and the visual sensitivity of the receiver, we might be able to predict how changes to the visual environment will influence the evolution of visual communication (Endler 1992; Gray and McKinnon 2007).

The *expression* of visual signals can be directly altered by environmental change, such as effects related to hormonal changes. As one example, exposure to synthetic oestrogens

found in fungicides caused a reduction in the size of carotenoid-based orange spots of male guppies (Baatrup and Junge 2001), a characteristic secondary sexual trait often favoured by females (Endler 1983) (Fig. 2, arrow 1). As another example, male three-spined sticklebacks (*Gasterosteus aculeatus*) exposed to endocrine-disrupting chemicals (EDCs) showed reduced aggressiveness and nest building activity, traits important for reproductive success (Bell 2001). Other effects on the expression of visual signals can stem from diet changes. For instance, the amount of forest canopy cover is negatively correlated with the availability of unicellular algae, which are an important source of dietary carotenoids in male guppies. A change in canopy cover could therefore affect the expression of a sexual trait of an aquatic organism and selection on it (Grether et al. 1999; Grether 2000; Schwartz and Hendry 2009).

The *transmission* of visual signals can also be altered by changes in water properties, particularly increasing turbidity (Fig. 2 arrow 2). Increased turbidity can be caused by sedimentary inputs (e.g., due to deforestation), and eutrophication through nutrient inputs (e.g., from agricultural runoff or sewage). Increases in both types of turbidity lead to a decrease in available ambient light (it becomes darker) and a shift in wavelength (the colour of the water changes), especially with depth and distance to shore (Evans et al. 2005; Donohue and Molinos 2009). In cichlid fish from Lake Victoria, the severity of eutrophication is negatively associated with the intensity of male colour, the strength of colour-mediated sexual selection, and the number of coexisting colour morphs and species (Seehausen et al. 1997; Seehausen et al. 2008; Maan et al. 2010, see Fig. 1a). Similarly, in three-spined sticklebacks, eutrophication weakens the strength of sexual selection on visual traits, increases the cost of mating, and allows dishonest visual communication of male condition (Candolin et al. 2007; Wong et al. 2007).

The *reception* of visual signals can also be altered because fish visual systems tend to be adapted to the spectral environment they inhabit (Loew and Lythgoe 1978; Levine and MacNichol 1982). For instance, visual performance in murky waters or deep sea conditions has been facilitated by the development of retinae with grouped photoreceptors (e.g., the elephantnose fish, *Gnathonemus petersii*; Landsberger et al. 2008). Sticklebacks have also been shown to have visual sensitivities matched to the local light environment, and linked with male nuptial colouration (Boughman 2001; Lewandowski and Boughman 2008). As a result of this local adaptation, environmental changes that influence signal *expression* and *transmission* should induce evolutionary or plastic changes in signal *reception*. Recent studies of East-African cichlids support this by suggesting that different light environments have led to the contemporary evolution of retinal pigments and their expression patterns (Hofmann et al. 2009). In addition, fish visual systems are often phenotypically plastic (salmon: Cheng and Flamarique 2004; killifish: Fuller et al. 2005; cichlids: Wagner and Kroger 2005; black bream: Shand et al. 2008; salmon: Temple et al. 2008), suggesting a capacity for changing environmental condition to initiate immediate morphological and physiological changes. However, whether or not fish visual systems can respond quickly enough to maintain effective communication during extreme anthropogenic changes is largely unknown. The collapse of Lake Victoria cichlid fish species suggests that there are limits to this (Seehausen et al. 1997, 2008).

Water flow is another property that can influence visual signalling (Fig. 2 arrow 3). For instance, male guppies in the headwaters of Trinidadian streams court readily in fast flowing riffles, whereas those from lower reaches prefer to court in slow flowing water (Kodric-Brown and Nicoletto 2005). Any change in flow regime is therefore likely to have consequences for male display and female preferences. Flow regimes can also influence extended visual phenotypes such as bowers and nests, used by some male fishes to attract

females. For example, in three-spined sticklebacks, a species in which females visually inspect nest characteristics prior to spawning for mate choice (Östlund-Nilsson and Holmlund 2003), the structure of nests built by males correlates with androgen-dependent physiological traits (Barber et al. 2001). Sticklebacks show both plastic and genetic responses to altered flow regime: in the laboratory, males from the same population can adjust their nest building to different flow conditions (Rushbrook et al. 2010); while sticklebacks from populations that evolved under different flow regimes show different nest properties even when raised in common laboratory conditions (Raeymaekers et al. 2010). In both cases, however, it is not clear whether these changes are a result of selection for more effective visual communication.

Chemical

Chemical signals play a large role in fish communication, facilitated by the solubility and propagation of chemicals in water (Sorensen and Stacey 2004). We know that fish use chemical cues, for example, in species recognition during mating (reviewed in Smadja and Butlin 2009), for making intersexual mate choice decisions within species (Wong et al. 2005; Milinski 2006), and for synchronizing reproductive behaviour (Sorensen and Stacey 2004). Changes to water properties will likely alter chemosensory interactions that currently contribute to the maintenance of species boundaries.

The potential for chemical signalling through water can be greatly affected by pollutants, involving signal *expression* acting through behavioural and physiological changes wrought by EDCs and other chemicals from waste-waters, pesticides from agriculture, and heavy metals from mining (Fig. 2 arrow 4; Table 1). Physiological changes, in particular, can alter the production of chemical signals and subsequent reproductive behaviours within an individual (Zala and Penn 2004). For example, exposure of male zebrafish (*Danio rerio*) to a synthetic estrogen caused a reduction in aggression and courtship behaviour (Colman et al. 2009).

The *transmission* of chemical signals will likely be influenced, in particular, by changes in flow regimes which will alter the delivery and environmental persistence of chemical signals (Webster and Weissburg 2009; Fig. 2 arrow 5). This is because hydrodynamics help determine the spatial and temporal availability of chemical cues, thus mediating chemical communication between individuals. Human-induced changes to flow regimes resulting from the construction of river impoundments, harbours and the canalization of waterways can change the efficacy of chemical signalling. For example, a moderate increase in water flow could help to disperse chemical cues over a greater spatial scale, increasing the range of attraction. On the other hand, a dam could cause a reduction in water flow, and thereby reduce the turbulent motion that typically disperses odour signals (Webster and Weissburg 2009). In sticklebacks, for example, this could be important as olfactory cues are likely used for long-distance mate attraction, while visual signals are used at short range (McLennan 2003). The evolutionary impacts of this kind of environmental change have not been studied.

Effects on chemical signal *reception* are also likely, but it is often not clear if the signal itself is disrupted (e.g. pollutants binding chemical signals) or if receptors are damaged and thus signal *reception* is altered. Much work has demonstrated that pesticides and other chemical pollutants can cause immediate plastic responses by the olfactory receptors of fishes, inhibiting *reception* of chemical cues (Zala and Penn 2004; Tierney et al. 2007). However, direct links between altered receptors and behavioural modifications are usually untested (Moore and Waring 2001; Jaensson et al. 2007; Tierney et al. 2007). Moreover,

almost nothing is known about the evolutionary consequences such changes might engender (Table 1). An exception was a study that showed disruption of female preference for conspecific male odour cues potentially leading to hybridization in the wild (Fisher et al. 2006). Evidence suggested a recent hybridization event between two closely related swordtail species in the Río Calnali (Mexico), *Xiphophorus birchmanni* and *X. malinche*, with the majority of hybrids descended from *X. birchmanni* females (Rosenthal et al. 2003). Fisher et al. (2006) experimentally confirmed that female *X. birchmanni* preferred conspecific over heterospecific males in clean water but lost this preference when tested using water from the river (i.e. polluted water, see Fig. 1b). Exposure to humic acid, a known fish pheromone binder found at elevated levels in water with high sewage input, elicited a similar loss of female preference for conspecific male odour cues (Fisher et al. 2006). It therefore seems likely that either a disruption of signal *transmission* or *reception*, and hence species recognition, may have led to the observed hybridization.

Although most research has emphasized a likely negative impact of altered chemical environments on fish communication (e.g. Moore and Waring 2001; Jaensson et al. 2007; Ward et al. 2008; see Table 1), some evidence for enhancement has been found. Heuschele and Candolin (2007) found that female sticklebacks were more attracted to male odour cues when the pH was increased to a level found in eutrophic waters. An increase in pH associated with eutrophication could therefore influence selection on male odour cues, which may be important because visual cues used for selecting mates will be disrupted under turbid conditions. Again in this example, it is not clear if the *transmission* of signals is disrupted or if the receptors are altered, thus affecting *reception* of the signal. These distinctions are important for predicting how selection on signals and sensory systems might operate under altered environmental conditions.

Acoustic

While little appreciated, fish have evolved a very diverse range of sound-producing mechanisms (Ladich and Fine 2006). Of these, the primary means for producing sounds involves vibration of the swim bladder through the contraction of sonic muscles (Ladich and Fine 2006). Most fish communication sounds are thus shaped by the physiology of the sonic muscles and the acoustic properties of the swim bladder. The sounds produced are typically low in frequency (<1000 Hz), pulsed, and repetitious (Amorim 2006). Variation in swim bladder sounds associated with different species or different social contexts are mainly caused by temporal changes in sonic muscle contraction patterns (Ladich and Fine 2006). Thus, sound variability is mostly based on differences in number and rate of sound pulses, although variation in the main frequency of the sound can also be found (e.g., there is often an inverse relation with fish size; Winn 1964). Most fish acoustic signals have a low amplitude and are predominantly produced at close-range during courtship and agonistic behaviours. Fish acoustic signals may play a major role in mate choice. For example, female pomacentrids prefer sounds of lower frequency that indicate a larger male body size (Myrberg et al. 1986). Such signals can also be important for species recognition, as shown in sympatrically occurring pomacentrids (Myrberg et al. 1978) and as suggested for Malawi cichlids (Lobel 1998; Amorim et al. 2004, 2008).

Changes in environmental characteristics that alter the behaviour or physiology of individuals have the potential to influence acoustic *transmission* and *reception*—although such effects have not been investigated. Anthropogenic sounds can be produced by boats/ships, construction activities (like pile driving), and active sonar (Fig. 2 arrow 6). Vocalization and hearing ranges of fishes can overlap with anthropogenic sounds

(Vasconcelos et al. 2007; Popper and Hastings 2009; Slabbekoorn et al. 2010) which could compromise the *transmission, reception and perception* of acoustic signals (Table 1). Exposure to anthropogenic noise can have a number of effects, including endocrinological stress responses, temporary or permanent hearing loss, and in extreme situations noise may injure or kill fish (Wysocki et al. 2006; Popper and Hastings 2009). The impact of noise pollution on fish communication depends on the duration and frequency of noise exposure (acute or chronic), degree of overlap of the sound frequency spectrum, and distance to the noise source. It can potentially impair the detection of conspecific courtship sounds because it can mask long-distance mate attraction calls (Vasconcelos et al. 2007; Popper and Hastings 2009). Even short term exposure to noise can be harmful in the breeding season but perhaps have no effect outside the breeding season. For example, initial investigations on the detectability of acoustic signals in the presence of ship noise revealed that, in the Lusitanian toadfish *Halobatrachus didactylus*, the auditory threshold increased significantly (Vasconcelos et al. 2007). A comparison of masked audiograms with the sound spectra of the mate attraction call of the toadfish, showed that ship noise decreased the toadfish's ability to receive conspecific sounds and therefore possibly the ability to find mates (Vasconcelos et al. 2007, see Fig. 1c). Even when mates are detected, noise could weaken mate choice based on courtship signals since they are typically quiet signals produced at close range (e.g. Ladich 2007; Simões et al. 2008) and the perception of variability related to male quality might be lost. The establishment of male hierarchies can similarly be affected. For instance, playback experiments carried out with the marine goby, *Gobius cruentatus* (Sebastianutto et al. unpubl.) have shown that exposure to recreational boat noise reduces the ability of resident males to define and maintain their territories, likely because acoustic communication is impaired.

We are only beginning to understand the role of fish acoustic signals in mate recognition, male-male competition, and mate selection. There is great need for further research on the biological significance of fish sounds and for well-controlled studies testing the effect of anthropogenic noise on fish (Vasconcelos et al. 2007; Popper and Hastings 2009).

Electric

Electric communication is relatively rare, with weakly electric fishes (African Mormyriformes and South American Gymnotiformes) making up a very small proportion of all fish diversity (about 1.5%; Moller 2006); however, the generation and sensory processing of electric signals has been the focus of a large body of neuroethological studies (for review, see Bullock et al. 2005). Weakly electric fishes generate electric fields by discharging an electric organ (Electric Organ Discharge, EOD), which creates an electric field around the body. By analyzing perturbations of this field, fish can detect the movements of potential prey items and recognize conspecifics vs. heterospecifics, males vs. females, and individual conspecifics (Zakon et al. 2002; Arnegard et al. 2006; Feulner et al. 2009; Fugère and Krahe 2010). Thus the expression and reception of electric signals are tightly linked within an individual.

Electrocommunication has been implicated, based on divergent EODs, as the main driver of diversification in several radiations of weakly electric fishes (Sullivan et al. 2002; Sullivan et al. 2004; Arnegard et al. 2005; Crampton and Albert 2006; Feulner et al. 2008; Lavoué et al. 2008; Feulner et al. 2009). Moreover, the evolution of EODs has been greatly influenced by ecological parameters (Crampton and Albert 2006). Fish with pulse-type EODs (brief pulses separated by longer and often variable pauses) can tolerate low oxygen, can quickly adjust to large temperature changes, and are often found in low-flow habitats.

In contrast, fish with wave-type EODs (pulses and intervals between pulses are of similar duration yielding a quasi-sinusoidal EOD) are highly sensitive to changes in temperature and are mostly found in fast-flowing, high-oxygen waters. EOD frequency increases with temperature (Dunlap et al. 2000; Silva et al. 2007), and it is unclear if the tuning of electroreceptors (i.e. the *reception* of electric signals) shows a sufficiently similar dependence on temperature to avoid tuning mismatches when temperature changes. This would affect wave-type species more than pulse-type fish, because the former show narrow tuning of electroreceptors to the individual-specific EOD frequency (Hopkins 1976).

Variation in environmental factors, such as temperature (e.g., due to climate change, deforestation, or point source industrial inputs, Fig. 2 arrow 7) and conductivity (e.g., via chemical effluent, Fig. 2 arrow 8), can induce plastic changes in the *expression* of the EOD signal (Table 1). When exposed to rapid changes in conductivity, the waveforms of the EOD of two African mormyrids (*Campylomormyrus tamandua* and *C. rhynchophorus*) were shown to change drastically, but returned to its normal shape within about two days (see Fig. 1d; Kramer and Kuhn 1993). In an experiment across a range of natural variation in conductivity, Baier (2008) also observed changes in the waveforms of sibling species (*Pollimyrus castelnaui* and *P. marianne*), but the species-specific differences between their signals remained stable. These findings suggest that changes in water conductivity may have only minor impacts on the recognition of species- and sex-specific electric signals. Increases in conductivity, however, lead to considerable shrinking of the spatial range of electrocommunication, which is likely to reduce perceived population density (Squire and Moller 1982). The effect of simultaneous changes to water conductivity and temperature on EODs has yet to be explored, as well as the effect of altered flow regime (Fig. 2 arrow 10); however, all are likely to affect EOD-based interspecific interactions, territorial behaviour, or mate choice.

Electropollution (e.g. electrical noise from power generators; Fig. 2 arrow 9) might be the best example of human-induced environmental change that could directly influence the *transmission* of electric signals. Similar to the masking effect of noise pollution, electrical line noise at 50 or 60 Hz (depending on the country), and its associated harmonic frequencies, overlaps with the EOD frequencies of many species. Further, undersea power cables, such as those from off-shore wind farms, might interfere with the electrosense of fishes, such as the round stingray, for whom a role of its passive electrosense in mate detection has been shown (Tricas et al. 1995). However, currently there are no data to support this idea of interference of electropollution with communication.

Expected effects of environmental change on weakly electric fish include shifts in electric signal properties and receptor tuning, local to regional changes in community composition, and/or the breakdown of communication-based reproductive isolation. Direct empirical research is needed to test for evolutionary consequences of environmental change on weakly electric fishes.

Multimodal communication

Traditionally, researchers have focused on only a single sensory modality at a time, either under the assumption that one modality will be considerably more important than others (Lim et al. 2008), or due to logistical constraints. However, it is generally recognized that multiple sensory modalities are frequently employed, as revealed in studies of mate selection in several species (reviewed in Candolin 2003). Given that the costs and benefits of different modalities will depend on the environmental context, fish may alter their use of, and dependence on, specific modalities during environmental change. For instance,

Heuschele et al. (2009) found that the relative importance of visual and olfactory cues in determining the mate preference of female three-spined sticklebacks differed in clear vs. turbid water. The information conveyed by each type of signal, and the specific males that were preferred, differed under the two modalities, suggesting that environmental perturbation can alter the form of sexual selection in this species.

The potential for environmental change to alter the relative importance of different sensory modalities also seems likely in other species. This might be especially true for species where multimodal communication is known to be important. For example, mate selection in Lake Malawi rock-dwelling cichlids depends on visual (Jordan et al. 2003; Pauers et al. 2004; Kidd et al. 2006), chemical (Plenderleith et al. 2005), and acoustic (Amorim et al. 2008; Smith and van Staaden 2009) cues. This does not mean that similar effects would not be important for species where one sensory modality generally predominates. For instance, weakly electric fishes tend to be found in habitats that impair vision and are mainly nocturnal. Despite this limitation, most species have the ability to use vision and other senses (see Moller 2002; Schuster 2006). Mormyrid fish possess functional retinae and can discriminate visual movements (Wagner 2007). Schuster (2006) explored the potential integration of multiple senses in weakly electric fish and proposed that constraints on electric signalling (e.g., range, electrical noise) could be overcome with the integration of multiple sensory modalities.

In short, a multimodal research approach could be important in all fish systems, especially as the frequency and severity of environmental perturbations increase with human activity. Changes to the benefits of relying on different sensory modalities would be expected to dramatically change the direction and targets of selection, altering evolutionary trajectories within species and the potential for the maintenance and production of new species.

Discussion

Evolutionary responses

Environmental changes are known to influence fish communication systems and diversity—as shown in the above examples. Many of these effects clearly represent phenotypic plasticity in that they are seen in *individuals* who experience environmental change. Genetic (evolutionary) changes are less well known, but are obviously possible on long time frames given the observed matches between species-specific traits and their local environments (Seehausen et al. 2008; Hofmann et al. 2009), as well as differences between conspecific populations raised in common laboratory environments (Lewandowski and Boughman 2008). As one example, cichlids from the relatively turbid waters of Lake Victoria (i.e., reduced transmission of visual signals) only express a subset of their opsin genes compared with the cichlids from the clear waters of Lake Malawi (Hofmann et al. 2009). As another, cave forms of several fish species have lost the use of their eyes (*Astynax mexicanus*: Jeffery 2005; *Poecilia mexicana*: Plath et al. 2008). At present, however, it is largely unknown to what extent communication systems will evolve in response to environmental change on contemporary time scales. In principle, this seems possible given that many other phenotypic traits do evolve on short time scales (Stockwell et al. 2003; Hendry et al. 2008).

Studies that document contemporary evolution of fish communication systems, however, are few—but informative. In particular, some studies have shown that environmental change can alter *selection* on communication systems—although evolutionary responses

have not yet been confirmed. For instance, eutrophication weakens sexual selection on male traits in sticklebacks (Candolin et al. 2007), sand gobies (Järvenpää and Lindström 2004), cichlids (Maan et al. 2010), and pollution does the same for swordtails (Fisher et al. 2006). *Evolutionary* changes have been shown for male nuptial colour following human-caused environmental changes, such as in experimental introductions (Endler 1980; Kemp et al. 2008) but such evolution is not inevitable (Karim et al. 2007; Kemp et al. 2008). We highlight here that much work remains to be done to determine just how and when communication systems will evolve following environmental change.

Future directions

It is important to keep in mind that research on environmental change and impacts on fish communication has been limited to a few species only, and generalisations are difficult, if not impossible, to make. Even here, research effort has been biased towards signals that humans can most easily receive, namely visual cues. Even within the field of evolutionary vision research, it is only recently that we have begun to consider what an animal looks like to a conspecific in its own environment (e.g. Endler et al. 2005; Cummings 2007; Kemp et al. 2008; Seehausen et al. 2008), rather than relying on a human-based reception model. In short, we need more biologically relevant research on more species and more sensory modalities, alone and in combination, and with an emphasis on if evolutionary change follows alteration of the sensory environment.

Finding answers to some of the following questions will be integral to our understanding of how communication systems will respond to the drastic environmental changes being experienced globally.

- What is the role of phenotypic plasticity vs. evolutionary change in the response of communication systems to environmental change?
- Are communication traits more plastic than other traits (e.g., life history, morphology) that are also affected by environmental change, and is their impact on the maintenance of diversity greater?
- How important are the temporal and spatial scales and dynamics of environmental perturbation in causing evolutionary change?
- Are these changes reversible and if so, how long would it take?
- What role does the integration of sensory input from different communication modalities in the brain play in the ability of fish to respond to changing environments?
- Can we expect the evolution of more/less complex signals and sensory systems under changing environmental conditions?
- Can we make general predictions regarding size and direction of changes in communication-related traits, given a change in a particular environmental component, or are responses species- and population- specific?
- Are there qualitative and quantitative differences between natural and human-induced change and, if so, do we expect quantitatively and/or qualitatively different responses of fish communication systems?

Conservation

The implications of altered communication systems for population and species persistence are yet to be evaluated. The degree of spatial and/or temporal variability in the environment might influence whether or not a species persists. Environmental stressors have the

potential to change environmental heterogeneity. Increased heterogeneity could promote natural variation in populations (e.g. Gray et al. 2008). Phenotypic plasticity is thought to be beneficial in heterogeneous and fluctuating environments, whereas in stable environments, genetic variation would be favoured (Svanback et al. 2009). Plasticity will allow populations to survive in rapidly changing environments, but there may also be an associated cost to keeping this trait (DeWitt et al. 1998). Thus, the ability of populations to persist during environmental change depends very much on its severity and duration, as well as the intrinsic capabilities of the population to adapt.

Long-term and widespread exposure to human impacts may lead to homogeneous aquatic ecosystems globally, leading to a prediction of reduced aquatic biodiversity. Aquatic ecosystems around the world are becoming more turbid, warmer, deoxygenated, and chemically polluted, acoustically disturbed or are experiencing increasingly altered flow regimes. These effects are further exacerbated by climate change (Parmesan and Yohe 2003). The reduction in aquatic biodiversity is already staggering: at least 40 of 1061 North American freshwater fish species went extinct in the last century (Ricciardi and Rasmussen 1999), and globally, at least 30% of fish species are threatened (Darwall and Vié 2005).

In general, conservation efforts should be focused on minimizing and/or removing environmental stressors on aquatic ecosystems that degrade the sensory environment. Even if conservation efforts succeed, we cannot predict whether the ecosystem will recover completely or whether the direction of selection, and hence evolutionary trajectories, will change. There are some models from fisheries data that predict that recovery after heavy fishing is much slower than the response to fishing, and reversal after a harvest moratorium may be very difficult (Dunlop et al. 2009; Enberg et al. 2009), largely because human-induced selection is thought to be much stronger than natural selection (Hendry et al. 2008; Darimont et al. 2009). The likelihood and the speed of any recovery further depends on the severity, scale of the exposure to environmental stressors, and on ecosystem dynamics. Furthering our understanding of how communication in fishes is influenced by environmental stressors in the short term and on evolutionary time scales will be essential to guide future conservation efforts.

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